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EFFECT OF TERRESTRIAL MOLLUSC HERBIVORY ON *HOLOCARPHA MACRADENIA* (ASTERACEAE) SEEDLINGS IN CALIFORNIA COASTAL PRAIRIE UNDER DIFFERENT CLIPPING REGIMES

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ABSTRACT

Herbivory is generally overlooked as a factor influencing the viability of endangered plant populations in western North American grasslands. I conducted experiments to determine the effects of terrestrial mollusc herbivory for survival of a federally endangered, annual forb, *Holocarpha macradenia* (Santa Cruz tarplant), in California's coastal prairie. In addition, I utilized litter removal and clipping regimes from a continuing study of site-specific responses to evaluate the relationship between herbivory rates from terrestrial molluscs and disturbance regimes. I planted seedlings of *H. macradenia* into copper bordered quadrats that excluded molluscs and into non-copper bordered controls at two sites in California's coastal prairie. Three treatment regimes of vegetation clipping and litter removal were utilized. Herbivory damage was assessed using an ordinal scale every two weeks throughout the rainy season. Molluscs were also trapped and identified. Herbivory amounts were significantly less when molluscs were excluded from plots for all disturbance regimes; however, there was no significant difference in herbivory levels between the disturbance regimes. A significant amount of invertebrate herbivory on *H. macradenia* was by the non-native slug, *Deroceras reticulatum* (grey garden slug), and this herbivory significantly affected the survivability of *H. maradenia* seedlings in California coastal prairie.

Key Words: Coastal prairie, grasslands, herbivory, *Holocarpha macradenia*, Santa Cruz tarplant, terrestrial mollusc.

Many recent studies concerning California's coastal prairies have focused on management strategies for maintaining populations of native plants (Corbin et al. 2004). Strategies for maintaining native plant populations include prescribed fire (Belsky 1992; Davidson and Kindscher 1999; Hatch et al. 1999), soil disturbance (Belsky 1992) mowing (Davidson and Kindscher 1999; Hayes and Holl 2003a, b), and limited grazing (Belsky 1992; Menke 1992; Davidson and Kindscher 1999; Hatch et al. 1999; Hayes and Holl 2003a, b). Primary concern about conservation of native grasslands has focused on the influence of habitat destruction (Hayes 1998) and competition from exotic grasses (Hayes and Holl 2003b; Seabloom et al. 2003), with little regard to the effects of nonnative, mollusc herbivores on native plants. The experiment reported here examines the effects of herbivory by non-native, terrestrial molluscs on seedling survival of *Holocarpha macradenia* Greene, a federally listed, endangered, annual forb.

Anecdotal observations have indicated that a large component of herbivory of *H. macradenia* is at the seedling stage and by molluscs (G. Hayes, pers. obs.). With *H. macradenia* populations requiring management and with most remaining populations experiencing decline or interannual variability in numbers, my study evaluates the effect of mollusc herbivory on the viability of *H. macradenia* seedlings, a component not examined in previous studies.

Temperate grasslands have a high abundance of terrestrial molluscs (Crawley 1983; Hulme 1996). In California's coastal prairie, *D. reticulatum* Müller, a nonnative species from Europe, is particularly abundant and widespread (B. Roth, American Malacological Society, personal communication). Where endemic, studies examining the effects of herbivory by *D. reticulatum* have been performed (Rodriguez and Brown 1998; Scheidel and Bruelheide 1999a, b; Hanley et al. 1995a, b; Frank 1997; Hatto and Harper 1969). For many species of plants, these studies found that mollusc herbivory is an important factor affecting survivorship and abundance.

The amount of damage from herbivory to seedlings in grasslands may be more important than other forces affecting seedling survival (Dirzo and Harper 1980), with mollusc herbivory often comprising a significant amount of this damage (Wilby and Brown 2001; Hitchmough 2003). In addition, the accumulation of plant litter can be a major factor in species competition (Hayes and Holl 2003a, b). The accumulation of plant litter in grasslands may limit seedling survival by not allowing favorable conditions for growth (Milchunas et al. 1995), increasing susceptibility to fungal pathogens by extending the duration of free water on leaf surfaces for fungal spore adherence and germination (Bradley et al. 2003), and also by providing a moist, protected habitat for terrestrial molluscs (Maze, pers. obs; Hitchmough 2003). The relatively recent introduction of *D. reticulatum*, which probably took place when the Spanish began grazing cattle in California (B. Roth, American Malacological Society, personal communication), may be affecting species composition in California's coastal grasslands as it affect species' composition in its native range (Cottam 1986; Edwards and Gillman 1987; Hanley et al. 1995a). Because mollusc prefer plants at the seedling stage (Duthoit 1964; Byers and Bierlein 1982; Hanley et al. 1995b), have preference-based feeding (Dirzo 1980; Hanley et al. 1995b), and can be a major factor affecting plant population size and viability (Hanley et al. 1996; Scheidel and Bruelheide 1999b; Fenner et al. 1999; Fritz et al. 2001), this herbivory may have implications for *H. macradenia* survivorship and persistence of its now fragmented and threatened populations.

Competition is likely intense in California's coastal prairie (Stromberg et al. 2002), and any competitive advantage may have major implications for a species' population viability (Hulme 1996). This competition, coupled with herbivory, can have significant effects on the survivability of plants (van der Wal et al. 2000). These factors, in addition to evidence that slug herbivory is a potent force affecting community structure and plant performance (Hill and Silvertown 1997; Scheidel and Bruelheide 1999a, b, 2001; Fritz et al. 2001; Buschmann et al. 2005), raise the question of to what extent does slug herbivory, affect *H. macradenia* survivability?

Therefore, my research goals were to answer the following questions: 1) What is the extent and the effect of mollusc herbivory on *H. macradenia* seedlings? 2) Which mollusc species are herbivores of *H. macradenia* and are they native or introduced species? 3) Do grassland management strategies employing the clipping and removal of vegetation influence mollusc herbivory?

Materials and Methods

Study Species

Holocarpha macradenia is a federally endangered, glandular, annual plant of California's coastal prairie, with a growth habit that ranges from prostrate and branching to erect and monopodial. Small plants can produce a single flower head, while larger plants have a rigid main stem and lateral branches that grow to the height of the main stem (1–5 dm) and produce many flower heads. The leaves are larger and linear at the base of the plant (up to 12 cm), and are reduced up the stem. *Holocarpha macradenia* produces more central disk flowers than any related species (California Department of Fish and Game 2002).

Holocarpha macradenia is known from grasslands below 150 m in elevation. Historically, it occurred from northern Monterey County, north to Marin County. Currently known Santa Cruz tarplant populations are frequently associated with non-native grasses (e.g., in the genera *Avena*, *Bromus*, *Hordeum*, *Briza*, and *Vulpia*). Native associates include species of related Asteraceae, and of *Juncus* and *Danthonia* (CDFG 2002). Current *H. macradenia* populations are in flux and survival of the species is dependent on management strategies employed (Hayes 1998), although many management efforts to increase its numbers have met with limited success. With only 13 natural populations, effective management strategies for both protecting the remaining populations and for facilitating the reintroduction of *H. macradenia* are needed.

Experimental Design

I conducted research between December 2003 and April 2004, from the first substantial rains to the end of the rainy season, at two coastal prairie sites within 4 km of the ocean, and less than 150 m in elevation. The sites were separated by 25 km, north to south. I conducted my experiment in 52 m × 52 m enclosures that have been undergoing clipping and vegetation removal manipulations since 1998 (Hayes and Holl 2003a, b). Study sites were enclosed with fencing in the fall of 1998 to keep out cattle and feral pigs. Within these enclosures, Hayes and Holl randomly allocated 30, 7 m × 7 m plots with ten treatments. For my study, I utilized three of the ten treatments (described below). The two sites were: "Elkhorn", 36°52′4.3″N, 121°44′23.8″W (near the Elkhorn Slough reserve in Monterey Co.) and "UCSC", 36°59′5.5″N, 122°3′0.9″W (on the University of California at Santa Cruz campus). The Elkhorn site is about 200 m from one of the largest known natural populations of *H. macradenia* while the UCSC site has no known historical population.

At both sites, I utilized plots with three treatments of clipping and removal of cut vegetation: clipped 2 times a year, clipped 6 times a year, and untreated "control" plots (Hayes and Holl 2003b). Treatments were accomplished with a weed-whip and removal of cut vegetation with a rake after each clipping. Control plots were not manipulated. Clipping and raking regimes greatly reduced both vegetation cover and biomass, although these were not measured during my study.

For each clipping regime at each site I placed a treated quadrat, bordered with copper flashing, and a control quadrat delineated with string. All were 1 m^2 and contained 16 4-week old seedlings, evenly dispersed within the plot. Each plant was 23–26 cm from any neighboring seedling or the plot edge. I placed my quadrats in the southeasterly corners of the Hayes and Holl 7 × 7 m plots, 1 m from the corners. Each of the quadrats for this study was assigned separate plots from the Hayes and Holl study. To ensure accurate herbivory measurements, clipping and raking were suspended for each quadrat for the duration of my study.

Whereas previous experiments used the broad application of molluscicides as an abundance- and density-reducing tool (Hanley et al. 1995a; Rees and Brown 1992; Frank 1997), both the sensitive nature of these grasslands and the possible presence of unknown, native molluscs warranted another approach. I used 8.5 cm copper flashing firmly adhered to the soil layer using galvanized 16-penny nails to create a barrier around these quadrats. Terrestrial molluscs cannot cross copper (Grewal et al. 2003) and the flashing employed was manufactured for this purpose (U.S. Patent # 4,471,562). In addition to the copper flashing, slug traps were placed in each southeasterly corner of the treated (copper-bordered) quadrats. The slug traps were a pitfall type consisting of a buried 12 once aluminum can a third filled with a Pilsner type beer. The traps further decreased the density and abundance of existing and emerging molluscs within the manipulated plots and provided specimens for identification. Slug traps were originally also placed outside of the fenced enclosures to further examine the mollusc species present; however, these traps were unsustainable due to damage from cattle.

Experimental Procedure

Seed of *H. macradenia* was collected from stock plants and sown on November 18, 2003 at the University of California Santa Cruz, Thimann greenhouse. Seedlings were moved outside of the greenhouse 2 wk after sowing. The seedlings were outplanted on December 18th and 19th into the quadrats, as the local rains were becoming substantial. Measurements of the extent of herbivory on *H. macradenia* seedlings were taken every two weeks from January 3, 2004 to April 6, 2004, with each site being measured within 2 d of each other. Herbivory damage was assessed visually on an ordinal scale of 0 to 4, corresponding to 4 = 100%, 3 = 75%, 2 = 50%, 1 = 25%, 0 = 0% of the plant damaged. Mollusc herbivory was easily identified: signs included characteristic feces, mucus "trails", a hand lens revealed rasped margins of damage indicating radular-type herbivory, and often, especially after precipitation events, I observed slugs actively consuming the seedlings.

I measured vegetation height in each plot by dropping a paper plate onto the vegetation and measuring from the plate's center to the soil surface (Davis and Sherman 1992). I averaged vegetation depth and litter for all plots within each clipping regime at the start of the study: clipping 2 times a year, 5.75 cm; clipping 6 times a year, 4.0 cm; "controls", 16.3 cm. In "control" plots, vegetation litter was so thick from the five years of the Hayes and Holl study that no change in the height of the vegetation was observed during the duration of the study.

Statistics

Measurements were compiled for each plot by taking the mean levels of herbivory for all seedlings for each date, respective of manipulation or control for each clipping regime. SAS version 8.01 (SAS Institute, Cary, NC) was employed for the univariate repeated measures ANOVA with sampling date, slug exclusion, and clipping regimes as the independent variables. A separate univariate repeated measures ANOVA was also employed to test for differences in survivability of *H. macradenia* with slug exclusion as the independent variable.

Seedling mortality was examined by computing nonparametric estimates of survivor functions, stratified by site, after recording the fate of each seedling. For this analysis of survivability, SAS version 9.1.3 (SAS Institute, Cary, NC) was employed with LIFETEST procedures, which allowed for seedlings that experienced mortality due to non-mollusc factors or that were alive at the end of the study, to be right-censored. For these survivor functions, a log-rank test for homogeneity between treatments was performed.

Results

Both the Elkhorn and UCSC sites showed significantly less herbivore damage in the copper-bordered plots as opposed to the control plots throughout the study ($F_{1,7}$ = 8.44; P = 0.0198, Fig. 1), with the rate of herbivory increasing over time as the study progressed ($F_{5,40}$ = 3.42; P = 0.0283).

Differences in herbivory among clipping regimes were not significant with regards to levels of herbivory ($F_{2,11}$ = 1.79; P = 0.2285).

Analysis of seedling mortality indicated that terrestrial molluscs have significant effects on the survivorship of *H. macradenia*, (log-rank, Chi-square statistic = 53.31, P < 0.0001, Fig. 2). Analysis by the same statistical method but without stratification by site resulted in similar values (log-rank, Chi-square statistic = 55.15, P ≤ 0.0001). At the end of the study (107 d), the survival estimate for control seedlings at both sites was 13.5%, while the mollusc-excluded seedlings experienced 55.8% survivorship. The probability of survival decreased at a greater rate

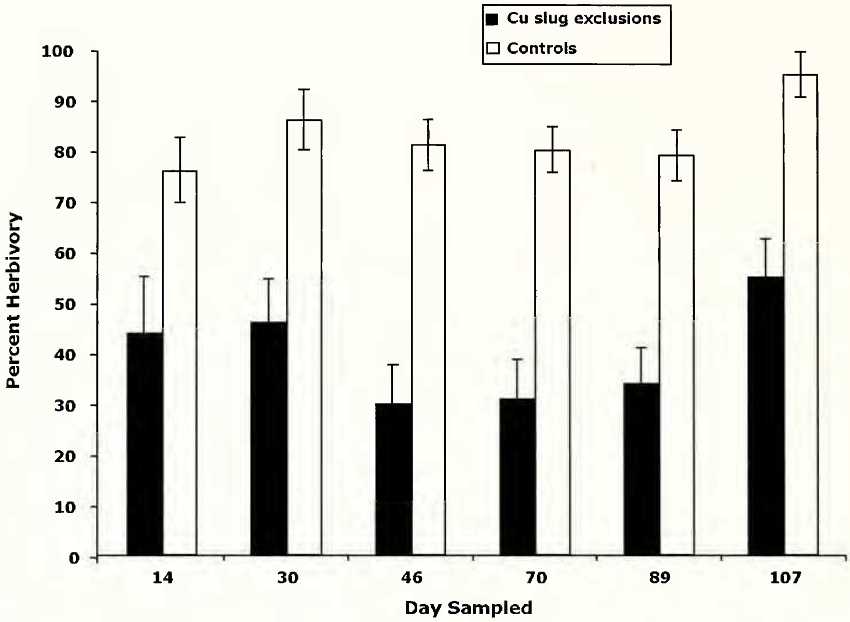

FIG. 1. Mean percent herbivory for all *H. macradenia* seedlings with regard to presence or absence of slug exclusions and without regard to clipping regimes. Error bars indicate standard error.

in control plots than in copper-bordered plots at both sites (Fig. 2), with estimated mean survival times reflecting this trend difference (Table 1).

DISCUSSION

The hypothesis that terrestrial molluscs significantly affect *H. macradenia* seedlings via herbivory is strongly supported by the results of this experiment. Exclusion and trapping of molluscs led to decreased rates of herbivory over the duration of the experiment with one notable exception, which was one copper-bordered plot at UCSC that underwent twice-yearly clipping. Initial rates of herbivory in this plot were statistically identical to that of the untreated

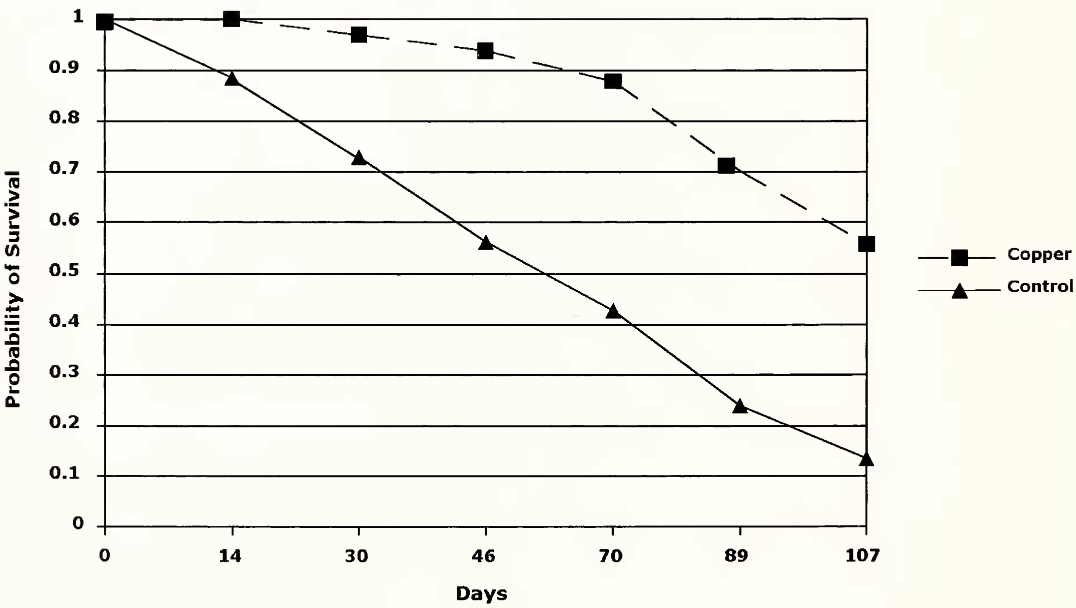

FIG. 2. Survival probability curves for mollusc-excluded (copper) and control seedlings. From a log-rank test for homogeneity, stratified by location.

TABLE 1. MEAN SURVIVAL TIME ESTIMATES (IN DAYS) AND STANDARD ERRORS FOR *H. MACRADENIA* SEEDLINGS AT BOTH SITES FOR MOLLUSC-EXCLUDED (COPPER) AND CONTROL SEEDLINGS. From a log-rank test for homogeneity.

	UCSC control	UCSC copper	Elkhorn control	Elkhorn copper
Mean survival time (days)	76.8	99.0	88.6	101.0
Standard error	3.03	2.14	2.08	1.98

controls due to a breach in the copper stripping of about 13 cm, which led to a large initial standard error for the combined means of the manipulated plots. The breach was due to cows which entered the fenced enclosure and damaged the copper barrier sometime between herbivory assessments. The copper barrier was breached for no longer than 13 d. The fact that the herbivory rates in the breached plot were so similar to those in the corresponding control plots is a testament to both the effectiveness of the copper (in light of the herbivory rates in the non-breached plots) and to the tenacity of the slugs themselves. After the repair, seedlings slowly recovered while the control seedlings of the corresponding plot were effectively decimated.

Seedlings performed differently at the two sites. The Elkhorn seedlings appeared more vigorous than their counterparts at the UCSC site, although statistical analyses showed that differences in herbivory and mortality were not significant. The Elkhorn site is next to a natural population of *H. macradenia* from which the seed for this experiment was collected. Two weeks after the last herbivory assessments were made most of the remaining UCSC seedlings had died, although seemingly not from invertebrate herbivory. Seedlings may have died because the site is not suitable for *H. macradenia*. Not all coastal grasslands are suitable habitat for *H. macradenia*, suggesting other factors such as soil type and microclimate should be considered for any reintroduction efforts.

Six of the 134 molluscs trapped over the duration of the study were not *D. reticulatum*. These were all one species of native snail and all were collected at the Elkhorn site in February. The snails were members of the family Succineidae, with the genus being either *Succinea* or *Catinella* which is associated with seasonally wet conditions (B. Roth, American Malacological Society, pers. comm.). These native snails are probably less effective herbivores than *D. reticulatum* based on the small number trapped and their diminutive nature (0.5 cm in diameter) relative to *D. reticulatum* (up to 8 cm in length in this experiment).

The impact of mollusc-induced mortality was perhaps the most striking result of this study. The survivorship curves illustrate the significant effect that mollusc herbivory had on *H. macradenia* in this study (Fig. 2). The fact that almost all herbivory was mollusc induced before day 70, and that one introduced mollusc was responsible for most (if not all) of this herbivory, suggests that *D. reticulatum* might be adversely affecting annual forb persistence in not only coastal but also interior grasslands (Severns 2006). Mollusc herbivory continued throughout the duration of the study with increased emergence of arthropod herbivores resulting in similar survival probability slopes between treatments after day 70 (Fig. 2); however, this was not statistically analyzed.

Mollusc herbivory was fairly constant with varying vegetation depth and clipping regimes until the last data set, where herbivory in the heavier thatched, non-clipped plots increased at UCSC (data not shown). This is perhaps due to the increasingly warmer and drier habitat as the rainy season ended. The fact that herbivory did not differ among clipping and vegetation removal regimes or controls earlier in the season might be due to the small size of the quadrats, unknown distance of movements of *D. reticulatum* in California coastal prairie, or ability of *D. reticulatum* to tolerate different amounts of cover and vegetation. This does not necessarily imply that in an unmanipulated setting, differences in disturbance history would not be important. Disturbance could affect the surrounding vegetation, which could then affect factors including germination time, seed mortality and predation, and seed dispersal. As for movements of *D. reticulatum*, in European rapeseed crops complete losses occurred within 2 m of slug habitat, although another species of slug was also present (Frank 1997).

Given that nonnative slug herbivory induced low survival for *H. macradenia* seedlings and that previous studies such as Bevill et al. (1999) illustrated that short-term protection of juvenile rare plants from invertebrate herbivores can improve the probability of long-term persistence of populations, future management of *H. macradenia* should examine possible ways to limit slug herbivory. Obviously, the cost, labor, and maintenance of copper flashing make this method highly impractical. More feasible methods include 5% metaldehyde pellets (a molluscicide), which is undesirable because of adverse impacts on native molluscs in the remaining remnants of coastal prairie in California. It was observed that a few (4 total) seedlings in heavily grazed control plots were never or only slightly grazed over the duration of the experiment, suggesting there might be a phenotype that resists mollusc herbivory as shown with *Asarum caudatum* (wild ginger) (Cates 1975). Results of this study suggest that *D. reticulatum* herbivory should be considered when devising management or reintroduction strategies for *H. macradenia*.

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